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STRUCTURE IN THE
SOLANACEAE

A DISSERTATION SUBMITTED TO THE FACULTY
OF THE DIVISION OF THE BIOLOGICAL SCIENCES
IN CANDIDACY FOR THE DEGREE OF DOCTOR OF
PHILOSOPHY

DEPARTMENT OF BOTANY

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By
MARY AILEEN MURRAY

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CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 570

MARY AILEEN MURRAY

Introduction

There has been much speculation on the exact morphology of the carpel and placentae in the Solanaceae. The axile placentae and cauline ovules ascribed to this family by most workers are difficult to reconcile with the Candolle theory that all floral parts are specialized leaves. According to the classic theory, an ovary is composed of one or more carpels, each of which is morphologically comparable to a folded leaf bearing ovules on its margins. In a syncarpous ovary, however, the carpels are undiverged, and the axis may extend into the gynecium. The problem is to determine whether the carpel walls, the septa, and the ovule-bearing portions of the placentae are cauline, foliar, or both.

A total of fourteen genera and twenty-one species of this family were selected for investigation, including members with fleshy and with only slightly fleshy placentae. On the basis of the anatomy of each flower, it was noted that WETTSTEIN's (23) phylogenetic arrangement of the genera agrees rather closely with a sequence based on floral anatomy. While this paper is not specifically one on phylogeny, the phylogenetic approach proved the best method of co-ordinating the material.

The Solanaceae contain many plants of economic importance. These can be divided into three groups. *Solanum tuberosum* (potato), *S. nigrum* var. *guineense* (garden huckleberry), *S. melongena* var. *esculentum* (eggplant), and species of *Lycopersicon* (tomato) and *Capsicum*

(pepper) are sources of food. *Nicandra physalodes* and species of *Lycium*, *Datura*, *Nicotiana*, *Petunia*, *Nierembergia*, *Salpiglossis*, *Schizanthus*, *Cestrum*, *Brunfelsia*, *Solanum*, and *Browallia* are cultivated as ornamentals. Several members are grown for the alkaloids they contain. These include *Atropa belladonna*, *Hyoscyamus niger*, *Datura stramonium*, and species of *Nicotiana*.

The flowers of the Solanaceae are hypogynous and generally actinomorphic, calyx four- to six-lobed and persistent, corolla sympetalous and generally five-lobed, stamens five, and the filaments adnate to the corolla and alternate with the corolla lobes. The ovary is usually bicarpellate, but in some plants there may be three to five carpels. The ovules are generally numerous and borne on more or less fleshy placentae. The fruit is a capsule or a berry. The Solanaceae are most closely related to the Scrophulariaceae but are separated from this family by having bicollateral bundles and an ovary which is oblique in relation to the median plane of the flower.

Among families in which the ovary is superior and bicarpellate and the corolla sympetalous, WERNHAM (22) lists the following tendencies: (a) actinomorphy to zygomorphy; (b) reduction in number of fertile stamens; and (c) reduction in number of ovules per carpel. The first two tendencies are particularly evident in the Solanaceae.

Material and methods

The plants listed were studied. The genera have been arranged according to

the classification of WETTSTEIN (23) in ENGLER and PRANTL's *Die Natürlichen Pflanzenfamilien*:

Nicandreae.....	<i>Nicandra physalodes</i> Pers.
Solaneae-Lyciineae.....	{ <i>Lycium halimifolium</i> Mill.
	<i>Atropa belladonna</i> L.
Solaneae-Hyoscyaminae.....	<i>Hyoscyamus niger</i> L.
	<i>Physalis alkekengi</i> L. (<i>P. francheti</i> Hort.)
	<i>Capsicum frutescens</i> L. var. <i>grossum</i> Bailey
	(Early Wonder)
	<i>Solanum tuberosum</i> L.
	<i>S. nigrum</i> var. <i>guineense</i> L.
Solaneae-Solaninae.....	{ <i>S. melongena</i> L. var. <i>esculentum</i> Nees.
	<i>S. pseudocapsicum</i> L.
	<i>S. dulcamara</i> L.
	<i>S. rostratum</i> Dunal
	<i>Lycopersicon pimpinellifolium</i> Mill. (included under <i>Solanum</i> by WETTSTEIN)
Datureae.....	{ <i>Datura stramonium</i> L.
	<i>D. meteloides</i> Dunal
	<i>Nicotiana sanderae</i> Sander (Crimson Bedder)
Cestreae-Nicotianae.....	{ <i>N. glauca</i> Graham
	<i>Petunia hybrida</i> Vilm. (Snowstorm-Giant Single)
	<i>Nierembergia hippomanica</i> Miers
Salpiglossideae.....	{ <i>Salpiglossis sinuata</i> Ruiz and Pav.
	<i>Schizanthus pinnatus</i> Ruiz and Pav.

The flowers and fruits were collected at various stages in development, killed and fixed either in Navashin's solution or in formalin-acetic-alcohol, dehydrated by the usual tertiary butyl-alcohol method, and imbedded in paraffin. Both longitudinal and transverse serial sections were cut at 12 μ , although some of the large fruits were sectioned at 20 μ . The material was then stained in a modified Flemming's triple stain.

Observations

Of the flowers studied, those of *Nicandreae*, *Solaneae*, and *Datureae* follow essentially the same pattern of floral anatomy. The exceptions are *Solanum rostratum*, which appears to be an anomalous form, and *Hyoscyamus niger*, which has slightly irregular flowers. All the oth-

er flowers are actinomorphic, the stamens are fertile and of equal size, and there are two adaxial bundles to each

carpel. *Physalis alkekengi* has been chosen as typical of this group.

The pedicel of *P. alkekengi* is an amphiphloic siphonostele; in the receptacle the vascular tissue consists of ten distinct bundles (fig. 25). The first five divergences extend outward and are the median sepal bundles. At the periphery, lateral divergences from the sepal bundles are anastomosed with one another (fig. 26). Slightly distal to the main sepal divergences, the vascular cylinder is again continuous. Next there are five petal divergences (fig. 26) alternating with the sepal bundles and accompanied by small parenchymatous gaps. At each side of the main petal bundle there is a lateral divergence, so that the corolla has fifteen prominent bundles in all. The vascular tissue is again continuous at a

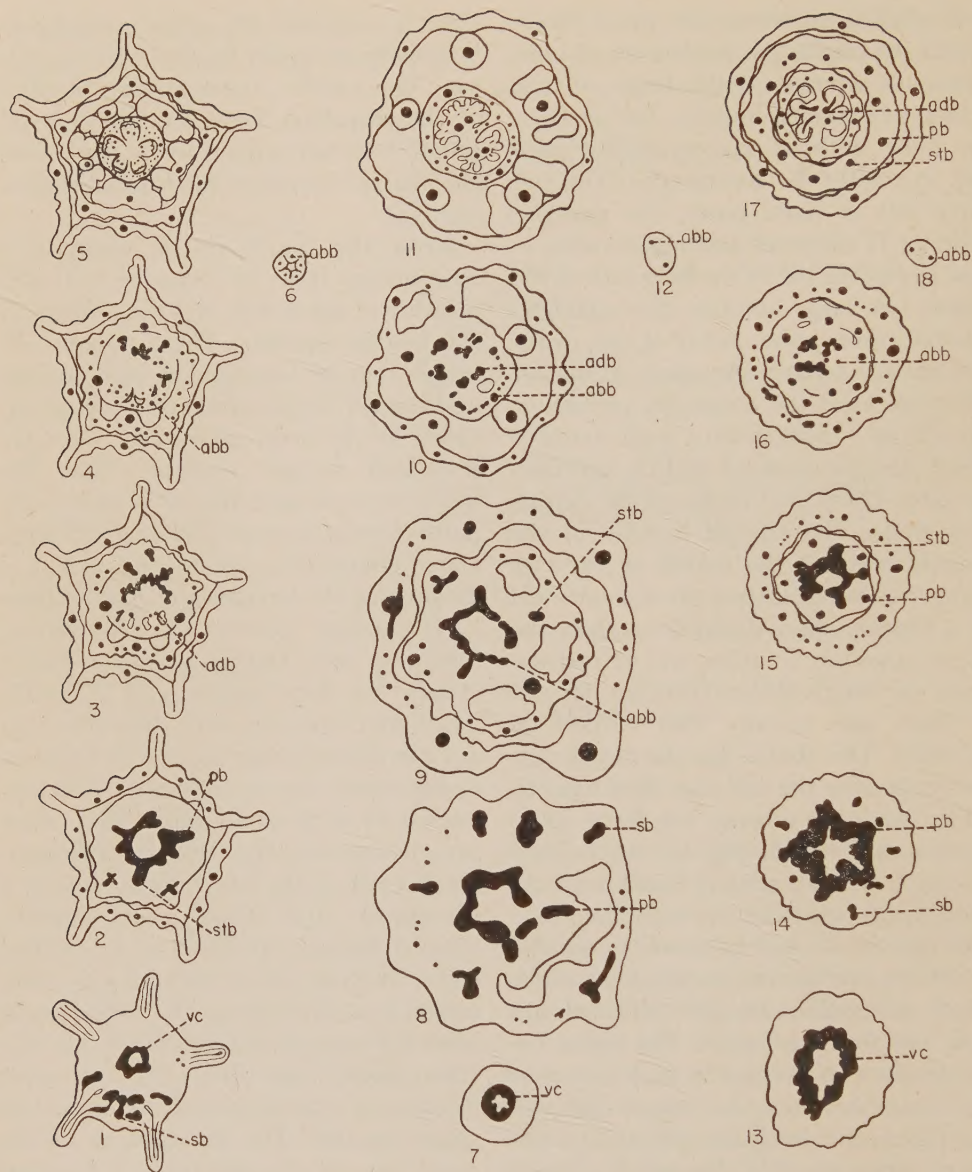
level slightly distal to the petal divergences. Opposite the median sepal bundles and alternate with those of the petals, five stamen bundles diverge from the stele without accompanying gaps (fig. 27). After the divergence of the first three sets of floral parts, the vascular cylinder is elliptical and again continuous. In the middle of the long arcs of the ellipse two large bundles (the adaxials) diverge toward the center of the ovary and are accompanied by gaps. At almost the same level the remaining portion of the ellipse is broken into small bundles which diverge outward slightly and then upward. These are bundles of the carpellary walls. The abaxial bundles of the carpels begin at the middle of the two short arcs of the ellipse, diverge outward at a slightly more distal level than the other carpellary bundles, and extend upward the length of the style (figs. 27, 28).

There are usually two carpels in *Physalis*. The abaxial bundle of one carpel is opposite the mid-bundle of a petal, while the other abaxial bundle is opposite a stamen bundle (fig. 29). At the level at which the two adaxial bundles are almost in the center of the ovary, four cavities become evident between the adaxial bundles and those of the carpellary walls. Then each adaxial bundle is divided into two, one for each carpel. The tissue between the two cavities in each carpel or the tissue between the carpel wall and the placenta extends for only a short distance. Distal to this, the ovary consists of the carpel walls, the two loculi, and two massive placentae bearing ovules which are supplied with vascular tissue through divergences from the adaxial bundles (fig. 29). At the top of the ovary the two septa do not meet completely, so that the uppermost portion of the ovary and the base of the style appear to be unilocular. Still farther up the style

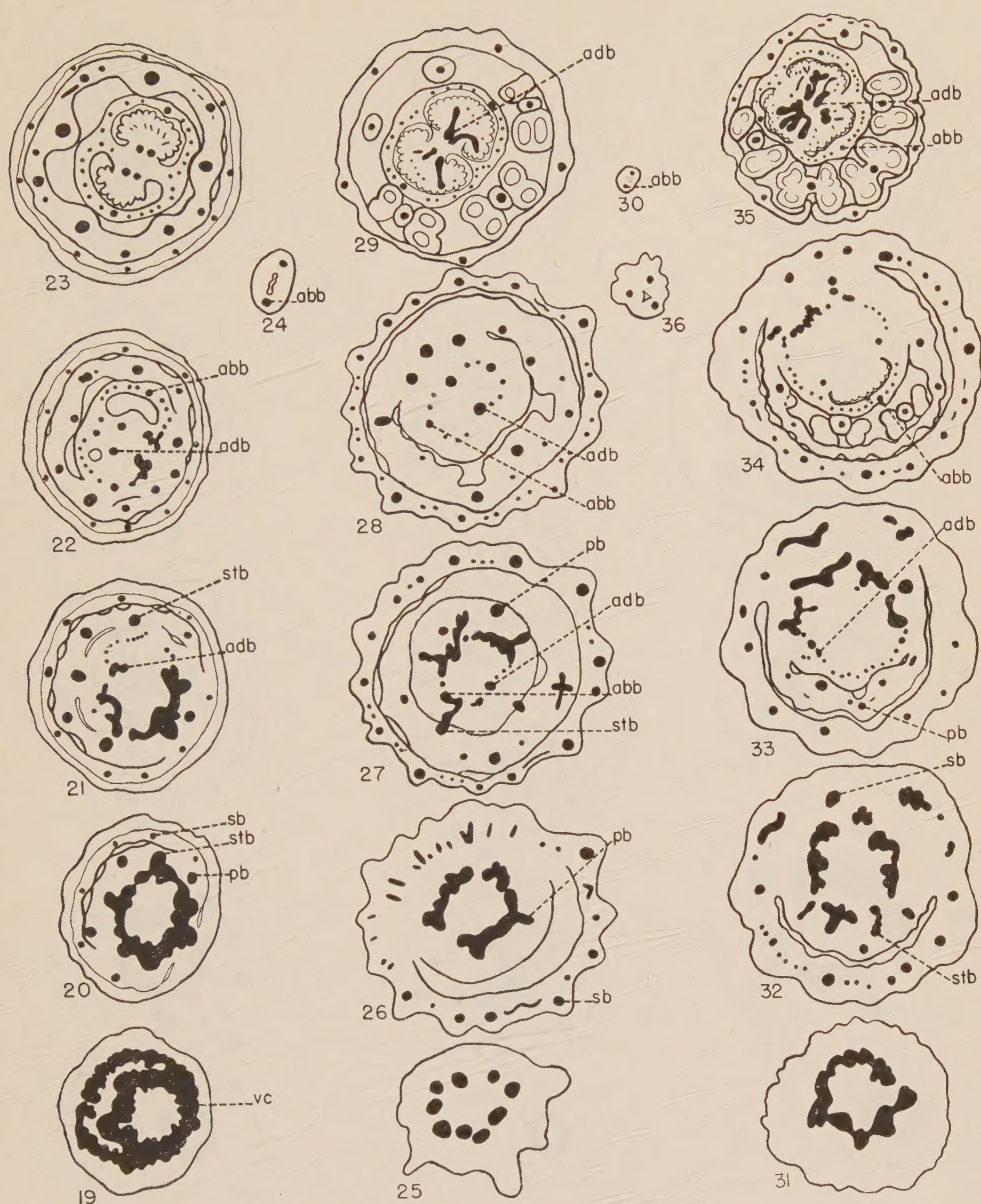
there is no cavity, the entire central portion being occupied by transmitting tissue. The smaller anastomosing bundles of the carpellary walls and the adaxial bundles are not present in the style, but the abaxial bundles extend to the stigma (fig. 30).

From the standpoint of interpretive morphology it is necessary to note the position of the xylem and the phloem in the adaxial bundles. These bundles diverge from an amphiphloic, siphonostele and remain bicollateral until they are divided at the level where the four cavities first become evident. Then the xylem is separated into two groups by parenchymatous rays, phloem is differentiated completely around each group of xylem, and the bundles are amphicribal.

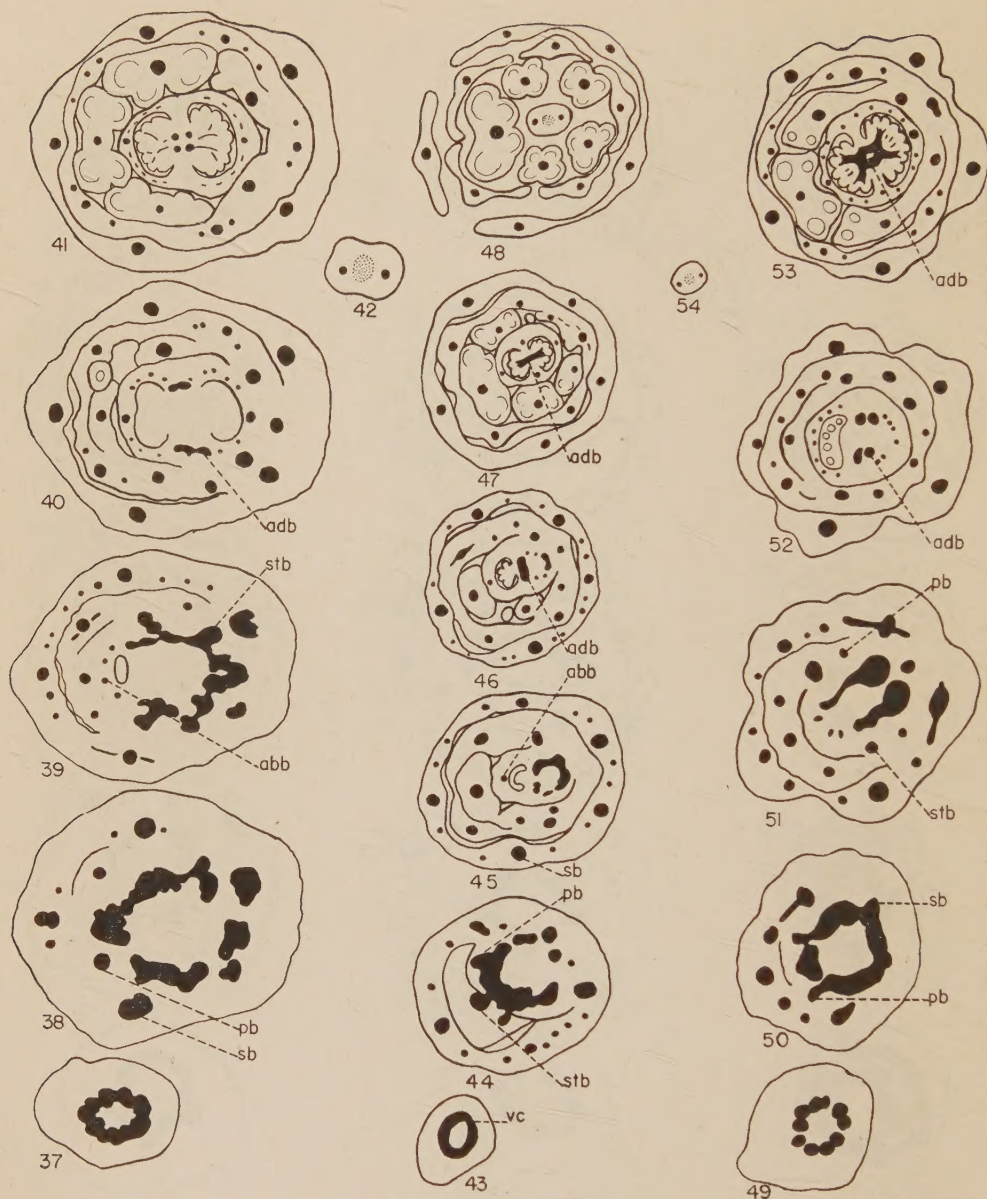
The other genera of Nicandreae, Solaneae, and Datureae follow rather closely the floral anatomy of *Physalis*. There are, however, some differences. In *Lycium halimifolium* the five divergences to the sepals may or may not be accompanied by very small gaps. After these first divergences, the stele is star-shaped. From each of the five points there is a divergence—the lateral sepal bundle. Smaller lateral bundles may be formed either through trifurcation of the main lateral or as divergences from this bundle after it is already differentiated (fig. 14). *Hyoscyamus niger* differs from all other Solanaceae studied in the formation of its sepal bundles. The divergences to the sepals are not separate traces but an entire ring of tissue. Certain portions of this outer cylinder stain darker and become differentiated into five large median, five large lateral, and an indefinite number of small anastomosing bundles. The ring of darker-staining tissue remains in the calyx and becomes lignified in the mature flower (figs. 19–23). *Capsicum frutescens* var. *grossum* and *Solanum melongena* var.



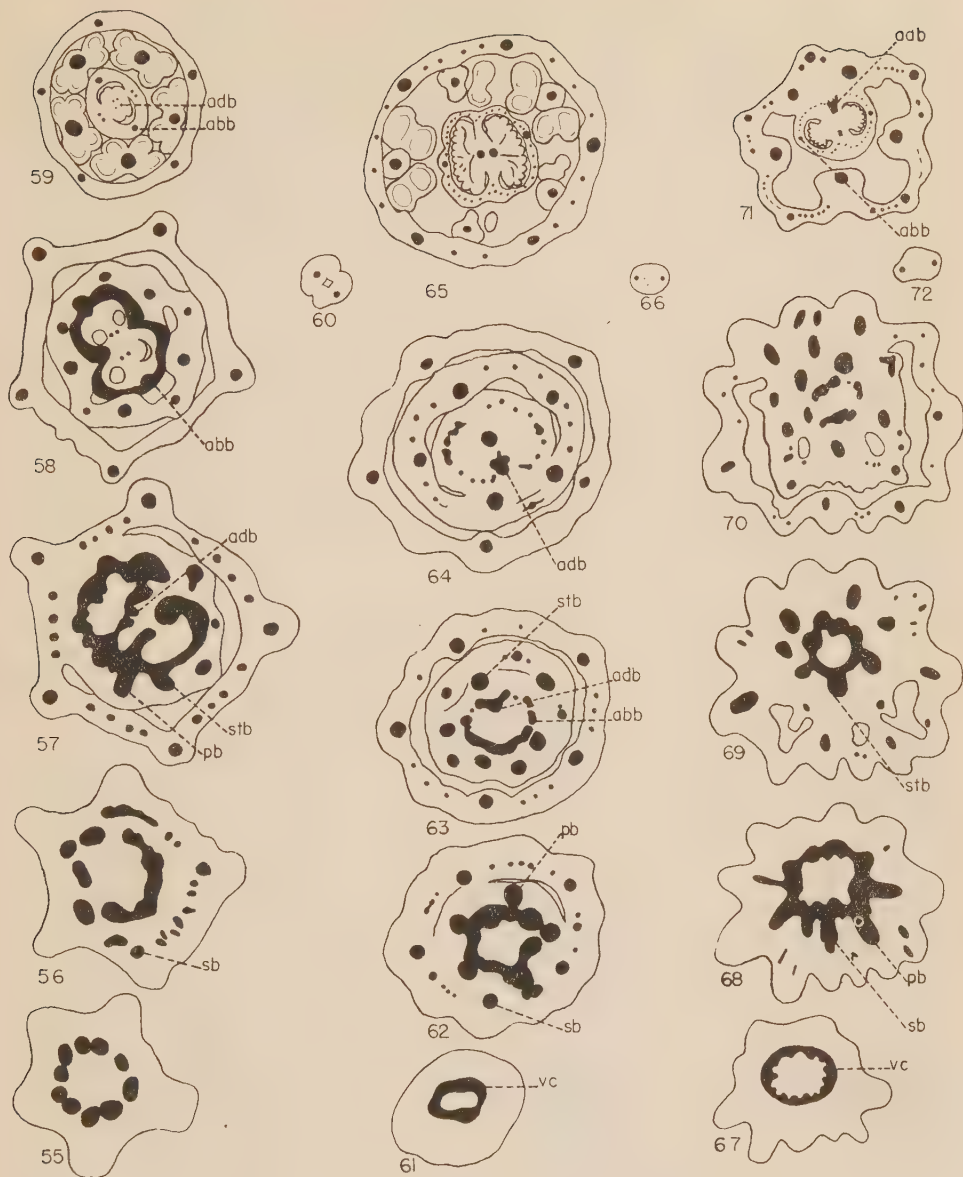
FIGS. 1-18.—Transsections of flowers from pedicel to apex showing comparable stages in floral development. Species in figs. 1-90 arranged in phylogenetic sequence. Figs. 1-6, *Nicandra physalodes*. Figs. 7-12, *Atropa belladonna*. Figs. 13-18, *Lycium halimifolium*. Figs. 10, 11, shown without sepals. Figs. 6, 12, 18, style. (vc, vascular cylinder; sb, sepal bundle; pb, petal bundle; stb, stamen bundle; adb, adaxial bundle; abb, abaxial bundle.)



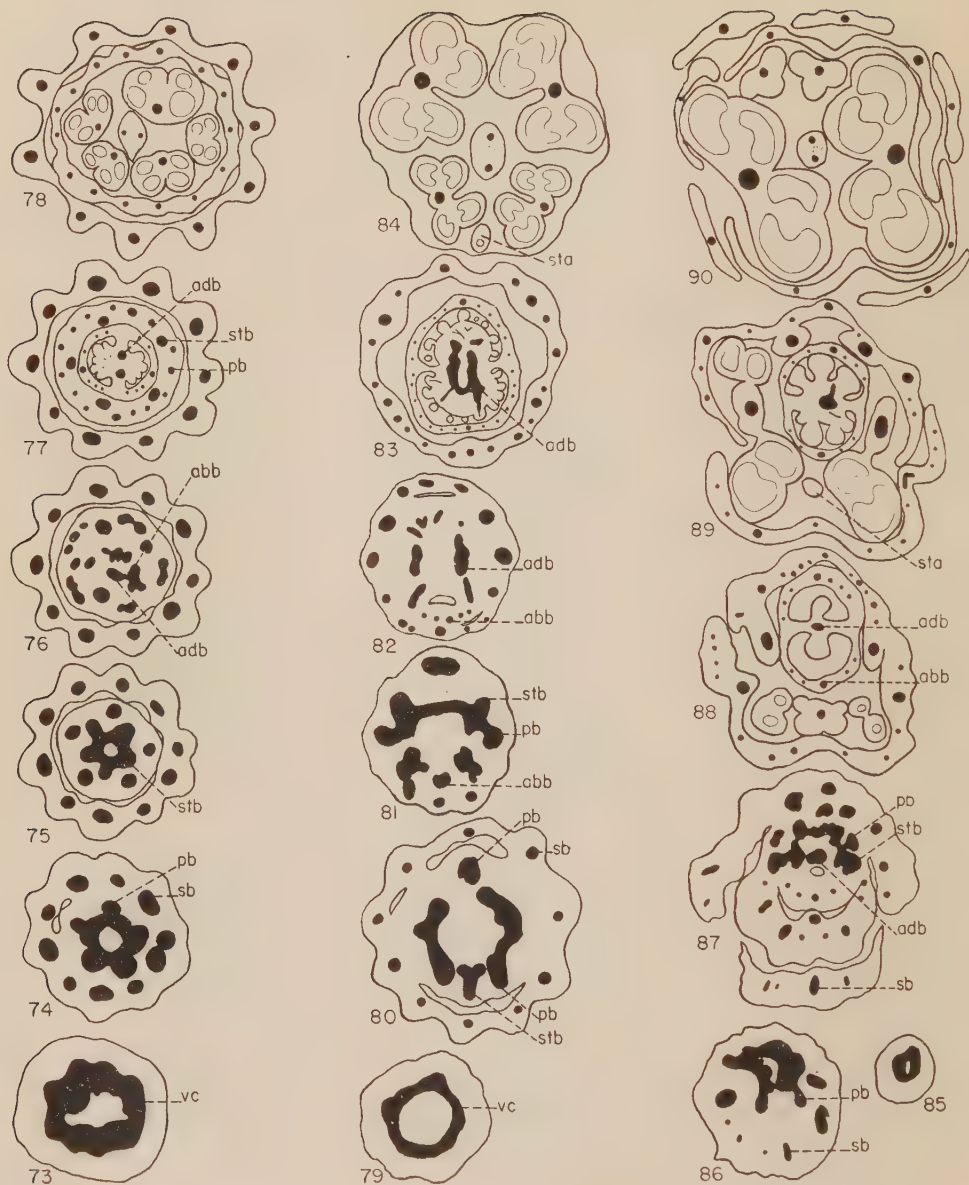
FIGS. 19-36.—Transsections of flowers from pedicel to apex. Figs. 19-24, *Hyoscyamus niger*. Figs. 25-30, *Physalis alkekengi*. Figs. 31-36, *Capsicum frutescens* var. *grossum*. Figs. 29, 35, shown without sepals. Figs. 24, 30, 36, style.



FIGS. 37-54.—Transections of flowers from pedicel to apex. Figs. 37-42, *Solanum tuberosum*. Figs. 43-48, *Solanum rostratum*. Figs. 49-54, *Lycopersicon pimpinellifolium*. Figs. 42, 54, style.



FIGS. 55-72.—Transsections of flowers from pedicel to apex. Figs. 55-60, *Datura stramonium*. Figs. 61-66, *Nicotiana glauca*. Figs. 67-72, *Petunia hybrida*. Figs. 59, 65, 71, shown without sepals. Figs. 60, 66, 72, style.



FIGS. 73-90.—Transections of flowers from pedicel to apex. Figs. 73-78, *Nierembergia hippomanica*. Figs. 79-84, *Salpiglossis sinuata*; figs. 81-83, shown without sepals; fig. 84, showing only stamens and style. Figs. 85-90, *Schizanthus pinnatus*; figs. 88, 89, shown without sepals. (*sta*, staminodium.)

esculentum are commercial forms. Because cultivation has brought about a multiplication of floral parts, the floral anatomy of these plants differs somewhat from that of the ancestral types. Pepper has six sepals (figs. 32-34), while egg-plant is even more variable. In most of the latter there are eight sepal divergences which do not come from the cylinder at the same level. These divergences are in two sets of four each, those of one set alternate with those of the other and at a level slightly distal to the first four. The anastomoses of the sepal bundles in *Datura stramonium* (fig. 56) and *D. meteloides* form an almost continuous ring of tissue between the main sepal bundles.

The differences in petal and stamen divergences require only brief mention. In *Lycium* (fig. 15), *Capsicum* (fig. 32), *Solanum dulcamara*, and *Lycopersicon* (fig. 50) the petal divergences are accompanied by parenchymatous gaps in the vascular cylinder, but no gaps are associated with the stamen divergences in any plant studied. The vascular cylinder does not again become continuous after the petal divergences in *Capsicum* (figs. 32-34). In the cultivated forms of *Solanum melongena* var. *esculentum* and *Datura meteloides* the number of petals and stamens is indefinite, and there is no sharp differentiation between these two floral sets.

The ovary of *Nicandra physalodes* usually consists of five carpels. The abaxial bundle of each carpel is opposite a petal bundle (fig. 4). In the formation of the carpellary vascular system from the stele, there are five outward divergences accompanied by gaps. These divergences are the abaxial bundles. Between each gap the remaining vascular tissue diverges outward and is divided into two strands. Each strand represents an adax-

ial bundle and several small bundles which are anastomosed through the carpellary tissue with the abaxial bundle. The two adaxial bundles which diverge together are for two carpels whose edges represent a septum common to both (figs. 3-5). When these adaxial bundles diverge they are bicollateral, but at more distal levels they are amphicribal.

In *Lycium halimifolium* a complete siphonostele remains after the stamen divergences (fig. 15). Two bundles opposite each other—the two abaxial bundles—diverge outward slightly and are accompanied by gaps. The remaining portion of the cylinder is broken into four equal arcs, each divided periclinally. The bundles of the carpellary walls diverge from the outer portion of each arc, while the inner parts of the four arcs diverge toward the center of the ovary and are the four adaxial bundles (figs. 16, 17). Since these periclinal divisions of the stele are through the xylem, each adaxial bundle has xylem facing the loculus and phloem centrad to the xylem. At more distal levels the bundles become amphicribal.

The carpel bundles of *Atropa belladonna* are derived from a stele in the form of an ellipse (fig. 9). In the two short arcs two bundles diverge outward slightly and are the two abaxial bundles. From the long arcs of the ellipse two large central bundles on each side diverge inward and are the four amphicribal adaxial bundles (figs. 9-11).

The cultivated variety, *Capsicum frutescens* var. *groszum*, has a three-carpellary ovary. The three abaxial bundles diverge from the vascular tissue centrad to three alternate stamen divergences. The inner portions of the other three stamen divergences form three adaxial bundles. At the level at which the three loculi can first be distinguished, the three adax-

ial bundles are in the septa. Then each adaxial bundle is divided into two, one for each adjacent carpel (figs. 33-35).

The carpellary anatomy of *Solanum tuberosum* (figs. 39-41), *S. nigrum* var. *guineense*, *S. pseudocapsicum*, *S. dulcamara*, and *Lycopersicon pimpinellifolium* (figs. 51-53) is similar to that of *Physalis*. In *S. nigrum* and in *L. pimpinellifolium* (figs. 53) the four adaxial bundles form an almost continuous cylinder of vascular tissue. No attempt has been made to interpret the ovary of *S. melongena* var. *esculentum*. Such an explanation is difficult without access to the ancestral type. In the large fleshy gynecia of the cultivated forms the carpellary tissue is very much proliferated and somewhat distorted. The number of carpels is indefinite. Ordinarily there are five to six around a thick central mass of tissue, in which one to two additional carpels may be found. The latter may constitute another set of carpels produced from the axis, which has remained meristematic. Such additional sets of carpels are found in the navel orange, in many "double" flowers, and are not uncommon in the Solanaceae, having been observed in both pepper and tomato. The vascular supply to the carpels of eggplant is derived from the siphonostele remaining after the stamen divergences. At a level just proximal to the formation of each carpel, the two adaxial bundles and the bundles of the carpellary wall diverge inward, so that the position of each carpel becomes first delimited by vascular tissue which is horseshoe-shaped. In the mature carpel there are two semicircles of vascular bundles around each carpel, and the ovules are borne on the placenta and also on what appears to be the carpel wall.

At the level at which the petal and stamen bundles diverge outward in

Datura stramonium, there are two inward divergences which are directly opposite each other, are accompanied by gaps, and are divided to form four strands of vascular tissue (fig. 57). These inward divergences are the four adaxial bundles, which differentiate as amphicribal bundles in the center of the ovary. After these divergences a continuous cylinder of meristematic tissue is formed (fig. 58). From it are differentiated two abaxial bundles, many small bundles in the carpellary walls, and two somewhat larger and distinct bundles in each of the septa (fig. 59). These last four bundles are probably not different from the bundles in the carpellary walls, but they seem to be much more distinct than the anastomosing bundles in *D. stramonium* and extend up into the basal part of the style. The lower half of the ovary and the fruit appears to have four carpels, resulting from the extension of tissue from the wall of each carpel to the placenta opposite the abaxial bundle. There are no vascular bundles in this tissue, however, and the structure seems to have no morphological significance.

The floral anatomy of the anomalous form, *Solanum rostratum*, resembles most closely that of *Schizanthus pinnatus*. The flowers show a marked tendency toward zygomorphy, with the large lower sepal and stamen differentiating before the other floral parts (fig. 44). This stamen is twice as large as the others (fig. 48). After the divergences to the first three floral sets, the vascular cylinder is divided into two abaxial, two prominent adaxial, and smaller bundles in the carpellary walls (fig. 45). The two adaxial bundles diverge from the periphery of the ovary to its center and fuse to form one adaxial bundle for the two carpels (figs. 46, 47). When the adaxial bundles are diverging, they are bicollateral; after they fuse, the

one bundle is amphicribal. *Solanum* is an extensive genus, and it is possible that evolution has taken place within the genus itself.

While the floral anatomy of the genera studied in Cestreae-Nicotianae and Salpiglossideae is basically like that of *Physalis alkekengi*, individual descriptions are necessary to explain the differences.

After the divergence of the two abaxial bundles in *Nicotiana sanderae*, the remaining carpellary tissue consists of a bundle adjacent to each abaxial bundle and two long segments of vascular tissue opposite each other and on alternate radii from the abaxial bundles. From the middle of each segment an adaxial bundle diverges toward the center of the flower and is divided. There are two amphicribal adaxial bundles for each carpel. In *N. glauca* the two adaxial bundles diverge toward the center of the ovary (figs. 63, 64). For a short distance they are fused to form one double bundle. Distal to this there is one adaxial bundle in the placenta of each carpel (fig. 65).

Each of the five sepal divergences of *Petunia hybrida* trifurcates to form one median and two lateral bundles (fig. 68). These sepal divergences are not accompanied by parenchymatous gaps, but small gaps may be associated with the petal divergences. While all the stamens are fertile, one is smaller than the other four. The cylinder remaining after the stamen divergences is divided into four segments—two large ones opposite each other and two small ones on alternate radii (figs. 69, 70). An abaxial bundle and two bundles for the carpellary wall are derived from each small segment. The large one is broken into several bundles for the carpellary wall and an adaxial bundle which diverges toward

the center of the flower. Each adaxial bundle may be double or divided into two bundles (fig. 71). In the mature ovary the adaxial bundles are amphicribal.

In *Nierembergia hippomanica* there are ten sepal divergences, which are not accompanied by gaps. Five of these are the main sepal bundles and five are laterals (fig. 74). When the calyx is separated into lobes, the laterals form a dichotomy with one branch to each adjacent lobe. The petal and stamen bundles are formed in the usual manner (figs. 74, 75). One to three of the five stamens are larger, but all are fertile (fig. 78). The last two stamen bundles to be diverged are opposite the two abaxial bundles. The remaining vascular tissue consists of two segments on opposite radii from the abaxial bundles. From these are diverged the two large adaxial bundles and part of the bundles of the carpellary walls (figs. 76, 77). The remaining bundles of the carpellary walls are lateral divergences from the abaxial bundles. Toward the distal end of the ovary the two adaxial bundles form one bundle, which is then divided into many small ones extending to the base of the style.

Salpiglossis sinuata shows a marked tendency toward zygomorphy and reduction in the number of fertile stamens. There are ten divergences to form five median and five lateral sepal bundles, as in *Nierembergia* (fig. 80). Only three of the ten bundles are accompanied by gaps. One of these is the sepal bundle in the lower lip opposite the staminodium. The other two such bundles are in the upper lip opposite the two large fertile stamens. After the sepal divergences the vascular tissue is usually continuous, although this state is difficult to observe because the lower lip of the flower differentiates at a more proximal level than the upper

part (fig. 81). The petal divergences are not accompanied by gaps. At the level at which the calyx is just diverged from the receptacle, the following bundles can be distinguished in the lower lip: three stamen, two petal, and an abaxial. At the same level the upper lip of the flower consists of one large petal bundle in the uppermost part and a semicircle of vascular tissue toward the center (fig. 81). When the bundles in the lower lip become differentiated, the remaining petal and stamen bundles diverge from the semicircle of vascular tissue in the upper part. There are two large fertile stamens, two small fertile ones, and a staminodium (fig. 84). Two strands of vascular tissue opposite each other remain between the lower and the upper parts of the flower (fig. 82). These diverge to the center and are the two adaxial bundles. At more proximal levels the adaxial bundles appear to be double, but at distal levels and in mature flowers the adaxial bundles are single and amphicribal, with only a slight tendency for the xylem to be separated into two groups by parenchymatous rays. At some levels the two adaxial bundles form an almost complete ring of vascular tissue (fig. 83).

Of all the plants studied, *Schizanthus pinnatus* is the most advanced. It is obviously zygomorphic, and the fertile stamens are reduced to two. In its floral anatomy, however, it still follows the same basic plan of all Solanaceae. The first divergence, the sepal bundle in the lower lip, is not accompanied by a gap. Slightly distal to this first sepal divergence and on either side of it are two petal divergences not accompanied by gaps (fig. 86). These petal divergences trifurcate; the two outer bundles are the lateral ones of the sepals, while the middle one is the petal bundle. Opposite the first sepal bundle there is a divergence to

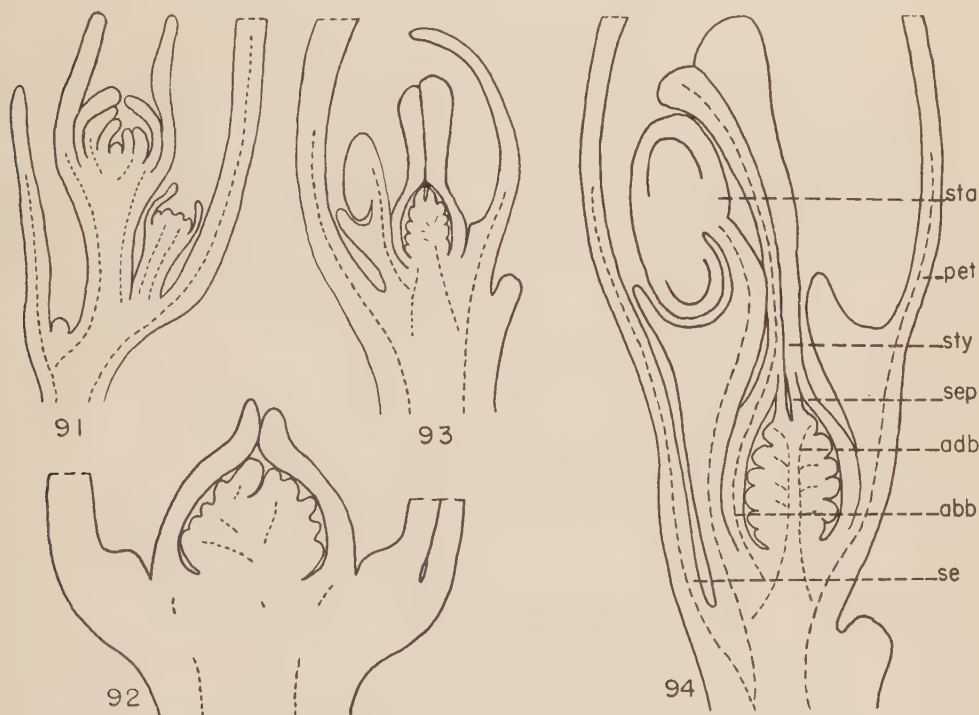
the most rudimentary of the staminodia. Only the filament of this stamen is formed, and there is rarely any indication of an anther (fig. 88). The divergences to the upper part of the flower are formed in the same manner but depart at more distal levels (fig. 87). The two stamens on either side of the vestigial one are fertile, and their anthers are very large in proportion to the other floral parts (fig. 90). The two uppermost staminodia develop small sterile anthers. After the stamen divergences, the vascular cylinder becomes solid. One to several cells in the center do not stain so dark as the surrounding meristematic vascular tissue. The outer part of this solid vascular cylinder is broken into a circle of small bundles which diverge outward and become the two abaxial bundles and the bundles of the carpellary walls. One abaxial bundle is directly opposite the most rudimentary stamen, while the other is between the two sterile stamens (fig. 88). The inner portion of the vascular cylinder does not change position but becomes the one adaxial bundle common to the two carpels (figs. 88, 89). At the level at which the ovules and placentae appear, one to several vessels become differentiated in the middle of the adaxial bundle. These vessels are the same in number as the large parenchymatous cells in the solid cylinder when it is first formed. The adaxial bundle is single, with no evidence of doubling, but at the top of the ovary this bundle may be divided.

The genera of Solanaceae can be separated into two groups according to the types of fruits produced. *Nicandra*, *Lycium*, *Atropa*, *Physalis*, *Capsicum*, *Solanum*, and *Lycopersicon* form berries, while *Hyoscyamus*, *Datura*, *Nicotiana*, *Nierembergia*, *Petunia*, *Salpiglossis*, and *Schizanthus* produce capsules. It is inter-

esting to note that, with the exception of *Hyoscyamus*, the more simple flowers develop into berries, while the more complex ones form capsules. Only in the first group is there much anatomical change from ovary to fruit.

In the fruit of *Capsicum frutescens* var. *grossum* the placentae are very much en-

proliferates and almost incloses each seed, but the tissues never actually fuse. The fruit of *S. melongena* var. *esculentum* is produced by enormous growth of the parenchyma of the placentae. The placental tissue of *Lycopersicon pimpinellifolium* proliferates greatly and almost entirely incloses each of the seeds.



FIGS. 91-94.—Successive stages in floral development. Figs. 91, 93, 94, *Nicot glanberglia hippomanica*. Fig. 92, *Physalis alkekengi*. (se, sepal; sep, septum; sty, style; pet, petal.)

larged, but this increase in size does not keep pace with the upward and outward growth of the pericarp and the septa. The placental tissue occupies a relatively small part of the loculi in the lower half of the fruit and is no longer fused with the lower portion of the style. The stylar end of the fruit is unilocular, since the septa are attached only to the pericarp. In *Solanum nigrum* var. *guineense* and in *S. pseudocapsicum* the parenchyma of both the pericarp and the placentae

In floral development the Solanaceous flowers included in this paper follow closely the descriptions of COOPER (4) and WARNER (21) for *Lycopersicon*, URQUHART (17) for *Lycium*, COCHRAN (3) and AUGUSTIN (2) for *Capsicum*, and YOUNG (25) for *Solanum tuberosum*. The sepals, petals, stamens, and carpels are formed in acropetal succession (fig. 91). While in longitudinal section the ovule-bearing tissue of the gynecium appears to be a prolongation of the axis, actually it

is axis plus carpellary tissue. The outer portions of the two carpels arch over the central axile prolongation and finally fuse (fig. 92). Continued elongation of the outer portions of the two carpels forms the style (fig. 93). At the apex of the central prolongation there is a depression, on either side of which the tissue grows upward and fuses with the basal part of the style (figs. 92-94). SATINA and BLAKESLEE (14) describe this occurrence in *Datura*. In the description of *Physalis alkekengi*, at the top of the ovary only the septal tissue remains. Finally the two septa are separated. The tissue which grows upward to fuse with the style is then the tissue of the two septa. The fusion of the septal tissue with the style differs somewhat in the various species studied. In *Hyoscyamus*, *Physalis*, *Capsicum*, *Nierembergia*, *Salpiglossis*, and *Schizanthus* ovules are formed before this fusion takes place, while in *Datura*, *Nicotiana*, and *Petunia* this fusion precedes the development of ovules.

Discussion

The syncarpous ovary, according to the Candolle theory, results from the fusion of carpellary leaves. The ovules are borne on the undiverged margins of these leaves, and the axis, if present, serves only as a support for these structures. There are many arguments for and against this theory. Before discussing them, it might be well to define the terminology used in carpel morphology.

The two principal types of placentation are axile and parietal. These terms generally apply only to position and have no morphological significance. Parietal placentation results when the ovules are borne on projections from the carpel wall. When the carpels fuse in the center of the ovary and divide it into as many loculi as there are carpels, the placentae are

axile. PAYER (12), STRASBURGER (16), and GRAY (7) are among those who state that with few exceptions all syncarpous, plurilocular ovaries have axile placentation. "Axial" and "cauline" refer to structures which are morphologically stem, while "foliar" applies to leaflike parts. The confusion in the literature arises from the use of positional terms in a morphological sense.

Among those who disagree with DE CANDOLLE and adhere to the axial theory are PAYER (12), SCHLEIDEN (15), and ST. HILAIRE (WORSDELL, 24). PAYER states that the "axile part of a syncarpous ovary constitutes the placentae and bears the ovules, while the carpellary leaves constitute the walls of the ovary." SCHLEIDEN states: "In all families with plurilocular ovaries one can easily follow the origin of the placentae which come from the axis." ST. HILAIRE also thinks that "the placenta is a continuation of and represents the axis." Between the axial and the appendicular theories is HAYWARD (9), who explains: "In the axile type of placentation, the placental tissue lies at the center of the ovary and may be foliar, or in part foliar and in part cauline."

Outstanding followers of the Candolle theory are VAN TIEGHEM (18, 19), HENSLOW (10, 11), EAMES (5), and ARBER (1). VAN TIEGHEM and HENSLOW are particularly helpful because they give definite criteria for interpreting the nature of the placentae. The following quotations are taken from HENSLOW. The first one (10) explains the views of VAN TIEGHEM, while the second one (11) gives the ideas of HENSLOW on the subject.

Van Tieghem in his investigations upon the anatomy of the pistil regarded the circle of vascular cords which have their trachae on the inner side, i.e. facing the medulla, and the

phloem on the outside of it, i.e. facing the cortex, as indicating the axis; but when the circle is broken up and these two elements of the cords are altered or reversed in position as they often are in the placentas of a carpel, he pronounced them to be "foliar."

The point, then, at which carpellary cords branch off from the common stem in the first case may be regarded as marking the termination of their axial character; and in the latter case, at the separation of the parts of the "horse-shoes" to form groups of threes. With regard to those cords which become marginal and placental, it is important to notice the position of their spiral vessels. If they are situated on the side of the cord nearest the medulla, the cord may generally be regarded as axial; if they are on the other side, i.e. nearest the ovary-cell, and if in transverse sections they exhibit intermediate positions, in which they are central or scattered irregularly within the phloem, they are then marginal and placental.

When floral parts are undiverged, the vascular anatomy seems to be the most valuable criteria for determining the origin of the parts involved. In this paper, therefore, the interpretation of VAN TIEGHEM and HENSLOW is used. If the adaxial bundles retain their stem-like character, with the xylem facing the center of the flower, the structures will be considered as cauline; if the xylem is facing the locus, or if the bundles are amphicribal, the structures will be considered as foliar.

As for the literature on the Solanaceae, PAYER (12), VIDAL (20), and RENDLE (13) describe the placentae as axile. In *Lycopersicon esculentum* var. *cerasiforme*, WARNER (21) explains the placentae as follows: "Apparently it is from the central more or less columnar axis that ovules arise. Thus they may be thought of as cauline in origin, or perhaps, the surface of this axis may be regarded as an undiverged portion of the sporophyll, in which case the ovules would be regarded

as foliar." URQUHART (17), working with *Lycium halimifolium*, states: "Although the placental structure is at this stage continuous with the carpellary tissue, it is largely cauline in origin. The ovules may be regarded as arising from cauline, axile placentae rather than foliar ones."

VIDAL (20) studied several species of the Solanaceae and concluded that in all of them the axis forms a thick septum raised to the summit of the ovary. In summarizing his work, VIDAL states: "The Solanaceae are characterized by a very well developed, parenchymatous axis raised to the summit of the ovary."

The most comprehensive paper on floral anatomy in the Solanaceae is by GRELOT (8). His emphasis is somewhat different from the present work, but on the whole the results agree. Concerning the adaxial bundles, he says: "If a certain number of bundles converge toward the center of the placenta and unite side by side to form a cylinder, the latter delimits a true pith whose role is different from that of the exterior parenchyma of the cylinder. One perceives then that the bundles take the same orientation as that in the stem." SATINA and BLAKESLEE (14), who worked with periclinal chimeras obtained in *Datura*, state: "The initiation and development of the carpel wall, septa, and placentae suggest that they are axial and not foliar in origin."

Of a rather different opinion is GOEBEL (6). He describes the development of the carpels as follows:

The process is exactly the same where we have in each locus a many-ovuled placenta developed as in Solanaceae and Scrophulariaceae. The ovary in its upper part is unilocular with two parietal placentas. . . . The carpels use up entirely the torus, and form to a certain extent a double sole, the septal wall. The margin of the cup of the ovary shows an increased growth at the points corresponding to

the apices of the carpels and the lateral parts raise themselves somewhat at the position of conrescence and there form the parietal part of the placenta. Beyond this the question of how far the flower-axis is drawn into the formation of the ovary is of quite subordinate importance.

The floral anatomy of the Solanaceae demonstrates that the placentae are

usually be distinguished. GRELOT's contention that such a cylinder is proof of the cauline nature of the placental bundles seems unfounded. The carpellary walls, the septa, and the ovule-bearing portions of the placentae are foliar in origin. The central fleshy part of the ovary is parenchymatous stelar tissue.

TABLE 1

Species	Type of flower	Stamens	Adaxial bundles	Fruit
<i>Nicandra physalodes</i> } <i>Atropa belladonna</i> } <i>Lycium halimifolium</i> }	Actinomorphic	All fertile	Two per carpel	Berry
<i>Hyoscyamus niger</i> } <i>Capsicum frutescens</i> }	Slightly zygomorphic	All fertile	Two per carpel	Capsule
<i>Solanum nigrum</i> } <i>S. melongena</i> } <i>S. dulcamara</i> } <i>S. pseudocapsicum</i> } <i>S. tuberosum</i> }	Actinomorphic	All fertile	Two per carpel	Berry
<i>Solanum rostratum</i>	Zygomorphic	1 large } fertile 4 small }	One for 2 carpels	Berry
<i>Lycopersicon pimpinellifolium</i>	Actinomorphic	All fertile	Two per carpel	Berry
<i>Datura stramonium</i> } <i>D. meteloides</i> }	Actinomorphic	All fertile	Two per carpel	Capsule
<i>Nicotiana sanderae</i>	Slightly zygomorphic	All fertile	Two per carpel	Capsule
<i>N. glauca</i>	Slightly zygomorphic	All fertile	Two for 2 carpels	Capsule
<i>Petunia hybrida</i>	Slightly zygomorphic	4 large } fertile 1 small }	Two double bundles for 2 carpels	Capsule
<i>Nierembergia hippomanica</i>	Slightly zygomorphic	1-3 large } fertile 4 2 small }	Two for 2 carpels	Capsule
<i>Salpiglossis sinuata</i>	Zygomorphic	2 large } fertile 2 small }	Two for 2 carpels	Capsule
<i>Schizanthus pinnatus</i>	Zygomorphic	1 sterile 2 large fertile 2 small sterile 1 vestigial	One for 2 carpels	Capsule

foliar in origin. In all the species studied the adaxial bundles in the older flowers and fruits are amphicribal and accompanied by gaps in the vascular cylinder. This applies even to *Schizanthus pinnatus* and *Solanum rostratum*, which have only one adaxial bundle. The occurrence of the adaxial bundles as a cylinder in the center of the ovary was noted in *Solanum nigrum*, *Lycopersicon pimpinellifolium*, and *Salpiglossis sinuata*, but the vascular tissue does not resemble an amphiphloic siphonostele and the individual amphicribal bundles can

In the Solanaceous flower the margins of the carpels are undiverged from the stem. At first there is conjoint growth of stem and carpels, but in the more mature flower the apical region of the stem ceases its meristematic activity. The exception is found in such plants as tomato, eggplant, and pepper, where growth continues to form a second fruit. Just how much of the ovule-bearing prolongation of the ovary is cauline and how much foliar would be difficult to prove. The adaxial bundles are foliar, and in longitudinal section they probably limit the

inner bounds of the carpels. The placentae are axile in position and foliar in origin. The Solanaceous flowers described in this paper can best be interpreted by the appendicular theory of DE CANDOLLE.

In general, the floral anatomy furnishes additional evidence of the validity of WETTSTEIN's arrangement of the genera. It would seem better to place the Hyoscyaminae at the end of the Solanaceae because the flowers of *Hyoscyamus* are slightly irregular and the fruit is a capsule. Among the Cestreae-Nicotianae and the Salpiglossideae there is a gradual reduction in the number of adaxial bundles per carpel. The phylogenetic tendencies of the Solanaceae described in this paper are summarized in table 1.

Summary

The floral anatomy of fourteen genera and twenty-one species of the Solanaceae was examined. The arrangement of the genera is according to WETTSTEIN in ENGLER and PRANTL's *Die Natürlichen Pflanzenfamilien*. In the order of their complexity, these genera include *Nicandra*, *Lycium*, *Atropa*, *Hyoscyamus*, *Physalis*, *Capsicum*, *Solanum*, *Lycopersicon*, *Datura*, *Nicotiana*, *Petunia*, *Nierembergia*, *Salpiglossis*, and *Schizanthus*. The following evolutionary tendencies were noted: actinomorphy to zygomorphy; reduction of fertile stamens from five to two; and reduction in the

number of adaxial bundles from two per carpel to one for two carpels. Despite these variations, the floral anatomy follows the same basic plan in all the species studied. The siphonostele generally becomes continuous after the divergences to each of the first three floral sets, and the carpellary bundles are formed from the remaining vascular tissue. Because the adaxial bundles are amphicribal and accompanied by gaps in the vascular cylinder, they are foliar rather than cauline. The placentae are axile in position, while the carpel walls, the septa, and the ovule-bearing portions of the placentae are foliar in origin. The central parenchymatous part of the ovary is stelar, and the carpels are undiverged leaves.

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